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Distribution of Oribatida (Acari) along a depth gradient in forested scree slopes

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Abstract

Mesovoid shallow substratum (MSS) of scree slopes constitutes a transition habitat between the soil and the network of voids in the vadose zone of a bedrock massif. In the present study, the vertical distribution of oribatid communities along a depth of 95 cm was studied at five forested MSS sites in the Western Carpathians, Slovakia. The sites differed in type of bedrock, topography and gradient of the microclimate and nutrients content. In all, 909 specimens were captured in subterranean traps exposed for one year. Most Oribatida represented edaphic forms, and their presence in the depth profile of the screes was accidental. *Pantelozetes cavatica* (Kunst, 1962) was the only species closely linked to deep subterranean environments found in the deeper part of the single limestone site studied. Species richness and the activity of oribatids along the scree profile at the sites clearly reflected the content of organic carbon in the soil substratum. The communities had very low numbers of individuals and low species richness at three sites with soil pH < 7 and organic carbon content in the upper soil layer ≤ 10%. However, they differed markedly in internal temperature dynamics. The other two sites, with a slightly alkaline soil pH and a higher carbon content, showed distinctly higher activity and a relatively uniform pattern of oribatid distribution across the depth profile. The soil pH and organic carbon content in the topsoil layer were substantial factors that determined the Oribatida diversity and vertical distribution in the forested screes.

Keywords

Environmental factors, mesovoid shallow substratum, oribatid mites, subterranean environment, vertical distribution

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Introduction

A shallow subterranean habitat represents an environment differing from deep caves by its close contact with the upper layers of soil (under 10 metres) and thus better access to nutrients (Růžička 1999; Moseley 2009; Culver and Pipan 2014). Colluvial 'mesovoid shallow substratum' (MSS) is a type of this aphotic habitat consisting of a network of cracks (voids) among rock fragments at the bottom of stony walls in steep mountain slopes (Juberthie et al. 1980; Juberthie 2000; Mammola et al. 2016). Such stone accumulations, also known as screes, stony debris or talus deposits, are often a frequent component of the relief in European mountains and form 'island habitats' (Růžička 1990; Růžička 1999; Barranco et al. 2013). Many authors have highlighted the presence of hypogean and epigean fauna in MSS but also specialized species that clearly prefer this environment (e.g., Růžička et al. 1995, 2012; Gers 1998; Giachino and Vailati 2010; Culver and Pipan 2014; Rendoš et al. 2016b).

The majority of the mite fauna in caves and subterranean habitats consists of Mesostigmata and Oribatida (e.g., Skubała et al. 2013; Jiménez-Valverde et al. 2015). Oribatid mites have a great potential to colonize MSS habitats due to their small body size and high density that they can reach in the forest soils, e.g. up to 200,000 ind./m^2 in boreal forests (Maraun and Scheu 2000). However, studies on Oribatida from subterranean environments are very rare, and only a few of them deal with the group in mesovoid shallow substratum. The first investigation of oribatid communities in MSS carried out by Arillo et al. (1994) in the Canary Islands led to the discovery of two new-to-science species. Much later, Skubała et al. (2013) detected that among Belgian speleofauna most oribatids were typical inhabitants of the upper layer of forest soil, and representatives of small oribatids, characteristic of deeper soil layers (e.g. Oppiidae), were rarely found. Recently, Nae and Băncilă (2017) described oribatid communities of an MSS site in the Romanian Carpathians, where common forest soil or tree-bark dwellers predominated. Similarly, Jiménez-Valverde et al. (2015) recorded three epigeic species of Oribatida when performing a study in Spain of subterranean fauna of bare scree slopes sparsely covered by the soil.

The present study was focused on Oribatida communities inhabiting the vertical gradient of five forested scree slopes in the Western Carpathians of Slovakia. Based on current knowledge, we assumed that the communities would differ noticeably along the environmental and nutrient gradients, and the differences in their structure would be closely related to changes in the environmental parameters of these screes.

The aims of the present study were: (1) to describe the distribution of oribatid communities along a vertical gradient at five scree sites in the Western Carpathians varying in topography and type of parent rock, (2) to clarify the presence of subterranean forms at these scree sites, and (3) to detect the response of the communities to environmental factors (internal scree temperature, soil pH and organic carbon content).

Material and methods

Study sites

Oribatida were sampled at five sites situated in different geomorphological units of the Western Carpathians in Central Europe (Fig. 1). The detailed site characteristics are provided in Table 1.

- Ardovská jaskyňa Cave (AJ) – a cave in the Slovak Karst near the village of Ardovo (south-eastern Slovakia). A southern scree slope with cornel-oak forest covered with soil and leaf litter and rocks with mosses, situated near the cave entrance. The scree profile: leaf litter and humus (0–15 cm), an organo-mineral layer with admixtures of small rocks and spaces partially filled with soil (15–75 cm) and a deeper scree layer formed by large rocks (75–100 cm).
- Belinské skaly Rocks (BS) – rocky locality in the Cerová vrchovina Highlands, near the village of Belina (south-eastern Slovakia). The site is a south-west exposed, carbon-poor volcanic scree slope with oak-hornbeam forest. The scree profile: leaf litter and humus (0–5 cm), an organo-mineral layer with a mixture of small basalt rocks and mineralized soil (5–70 cm) and a scree of small stones with spaces filled with soil (70–110 cm).
- Drienčanský kras Karst (DK) – a small karst area in the Revúcka vrchovina Highlands, near the village of Špánie Pole (south-eastern Slovakia). The site is formed by a limestone ridge and a steep north-facing scree slope with beech-hornbeam forest lying a few metres below the entrance of the Špaňopolská jaskyňa Cave. The scree profile: leaf litter and humus (0–5 cm), an organo-mineral layer and soil with tiny stones (5–70 cm) and a scree of bigger rocks partially clogged with soil (70–110 cm).
- Malý Ružínok Valley (MR) – a karst valley in the Čierna hora Mountains, near the village of Malá Lodina (eastern Slovakia). A massive limestone cliff with several short caves and a north-exposed scree slope with linden-maple forest at its base are the typical features of this site. The scree profile: leaf litter and humus (0–15 cm), an organo-mineral layer (15–45 cm) and a clearly separated scree of bigger stones with spaces partially filled up with soil (45–110 cm).
- Silická ľadnica Cave (SL) – a cave with the permanent floor ice at the Silická Plateau in the Slovak Karst, near the village of Silica (south-eastern Slovakia). A west-facing scree slope with hornbeam-maple-linden-oak forest is located in the sinkhole near the cave entrance with a dense herbal cover. The scree profile: leaf litter and humus (0–10 cm), an organo-mineral layer with well developed rhizosphere and spaces substantially filled with soil (10–35 cm) and an extremely stony scree (35–110 cm).

Sampling and species identification

At each site, a few metres below the top of the scree slope, a pit approximately 200 × 40 cm in area and over 100 cm deep was excavated, and the soil of the particular

Figure 1. Localities of samplings. 1 – Ardovská jaskyňa Cave, 2 – Belinské skaly Rocks, 3 – Drienčanský kras Karst, 4 – Malý Ružínok Valley, 5 – Silická ľadnica Cave.

layers was carefully separated. Three subterranean traps, after Schlick-Steiner and Steiner (2000), were vertically placed into the pit, 50 cm away from one another. The pit was subsequently backfilled with the dug-out soil and stones in the original order of the layers. The subterranean trap consisted of a plastic cylinder (length 110 cm, diameter 10.5 cm) with openings (diameter 0.8 cm) drilled around at 10 horizontal levels (5, 15, 25, 35, 45, 55, 65, 75, 85 and 95 cm), and a demountable system of 10 plastic cups (volume 500 ml), connected by a central iron rod and nuts. The buried cylinder served as a casing, allowing the insertion of cups filled with a 4% formaldehyde solution. The position of the cups inside the cylinder corresponded to the openings on the cylinder perimeter. The top of the cylinder was tightly closed with a plastic cap (Fig. 2). The subterranean traps at the Malý Ružínok Valley were exposed from October 2008 to October 2009 (366 days). The traps at the Belinské skaly Rocks and Drienčanský kras Karst were exposed from October 2012 to October 2013 (370 days) and at the Ardovská jaskyňa and Silická ľadnica caves from October 2014 to October 2015 (361 days). To remove the captured specimens, the system of plastic cups was pulled out of the buried cylinder, and the individual cups were dismounted. The contents of the cups were then poured into plastic bottles and transported to the laboratory for analysis. Oribatida were separated from the samples, mounted on temporary slides with lactic acid and identified using a Leica DM1000 light microscope and identification keys (Kunst 1971; Pavlitshenko 1994; Weigmann 2006).

At each sampled site, microclimatic and chemical parameters were collected from depths of 5, 35, 65 and 95 cm. The temperature was measured continually over the sampling period at 4-hour intervals using iButton DS1921G data-loggers mounted on the walls of the plastic cups. To determine the soil chemical parameters (pH and

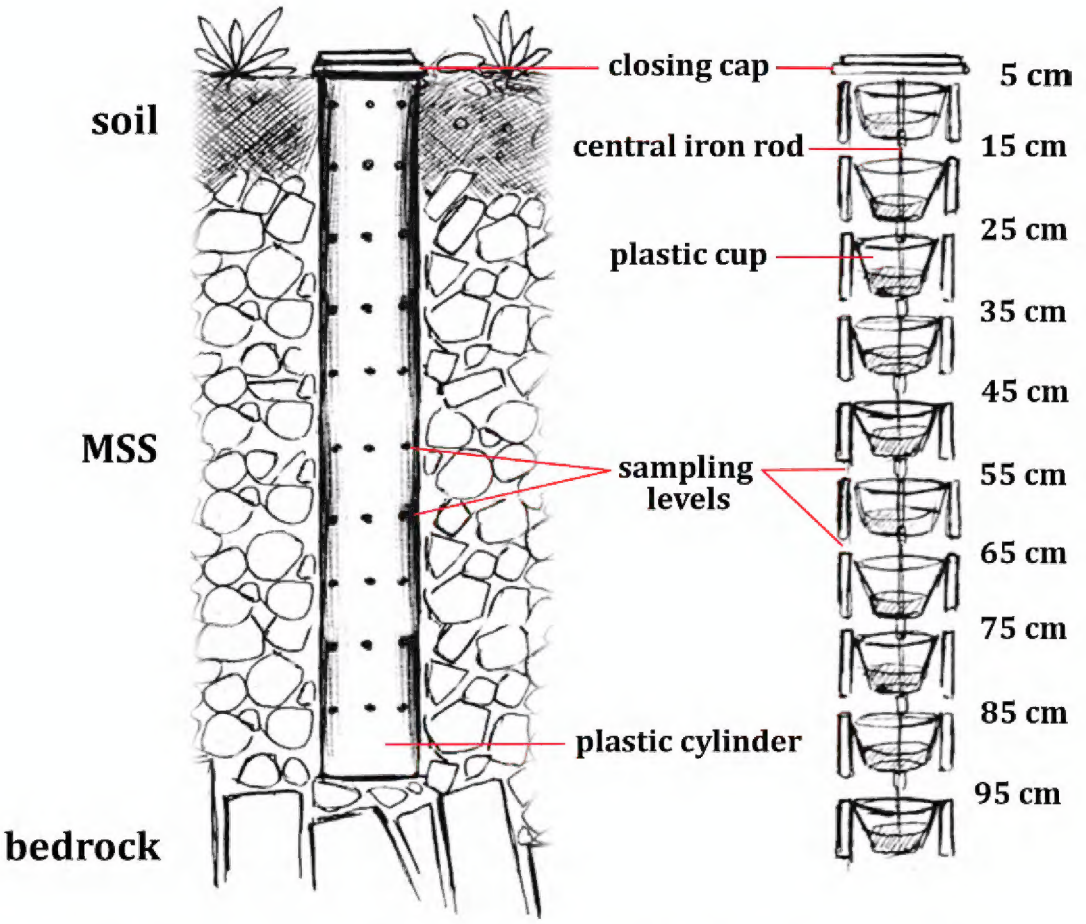

Figure 2. Subterranean trap design in MSS (modified after Mammola et al. 2016).

organic carbon content), soil samples were taken once during the excavation of pits, with a total of 20 samples analysed (5 sites × 4 depths). Samples were hand-mixed, and coarse particles, such as stones and vegetation remnants, were removed. In the laboratory, the samples were air-dried for several weeks and subsequently sieved (mesh size 2 mm). Soil pH was measured potentiometrically in a 1:5 soil:deionised water suspension, and organic carbon content was analysed using the dynamic combustion method (Carter and Gregorich 2008).

Statistical analysis

The Sørensen (qualitative) similarity index (Chao et al. 2006) and the Bray-Curtis (quantitative) similarity index (Magurran 2004) were calculated for each site to emphasize the community similarities along the depth profile.

Results

Site temperature regime and characteristics

The sites were defined by similar patterns of temperature regime. More variable temperature fluctuations were noted on the soil surface horizons (0–35 cm). Deeper in the

soil (55–95 cm), the fluctuations were slighter but synchronized with the climate dynamics near the surface (Fig. 3 and Table 1). The dependence between yearly temperature averages and soil depth showed various results at individual sites but a temperature was more stable with increasing depth (Table 1). The average internal temperature decreased gradually along the depth gradient at Ardovská jaskyňa and Silická ľadnica Caves, unlike the Belinské skaly Rocks, Drienčanský kras Karst, and Malý Ružínok Valley sites, where a temperature increase was observed (Table 1). The Belinské skaly Rocks site had slightly acidic soil, whereas the other four sites had slightly alkaline to neutral soil pH. The carbon content basically showed a decreasing trend with increasing depth, but it differed considerably between the individual scree sites (Table 1).

The dependence between monthly temperature averages and soil depth showed various results at individual sites but a temperature was more stable with increasing depth (Table 1).

Table 1. Topographic, microclimatic and soil-chemical characteristics of the study sites (soil type classification after the FAO system). T – average yearly temperature and standard deviation (monthly measures), pH_{H2O} – soil acidity, C_{org} – organic carbon content.

	Site				
	Ardovská jaskyňa Cave	**Belinské skaly Rocks**	**Drienčanský kras Karst**	**Malý Ružínok Valley**	**Silická ľadnica Cave**
Coordinates [DDM]	48°31.3'N, 20°25.2'E	48°13.3'N, 19°51.8'E	48°31.7'N, 20°07.1'E	48°50.5'N, 21°06.6'E	48°33.0'N, 20°30.2'E
Altitude [m a.s.l.]	317	460	315	530	455
Slope [°]	20–25	20	35	15	20
Exposition	SW	SW	N	NE	W
Bedrock	limestone	basalt	limestone	limestone	limestone
Soil type	rendzina	calcaric cambisol	rendzina	rendzina	rendzina
Forest composition	cornel-oak	oak-hornbeam	beech-hornbeam	linden-maple	hornbeam with *Acer campestre*, *Tilia* sp., *Quercus* sp.
T [°C]					
0 cm	10.2 ± 6.6	8.9 ± 7.4	–	8.1 ± 6.0	–
15 cm	9.9 ± 5.4	9.5 ± 6.6	8.0 ± 5.7	8.7 ± 5.2	8.0 ± 5.3
35 cm	10.3 ± 4.8	9.7 ± 5.6	8.2 ± 5.2	8.8 ± 4.9	7.8 ± 4.8
55 cm	9.6 ± 4.4	9.1 ± 4.9	8.2 ± 4.8	9.2 ± 4.6	7.7 ± 4.1
75 cm	9.9 ± 4.1	9.7 ± 4.6	8.5 ± 4.4	–	7.6 ± 3.9
95 cm	9.8 ± 3.7	9.6 ± 4.1	8.3 ± 4.1	9.3 ± 4.0	6.6 ± 3.6
pH_{H2O}					
5 cm	7.3	5.0	6.6	7.7	6.7
35 cm	7.9	5.6	8.1	8.2	7.4
65 cm	8.1	6.3	8.2	8.2	7.8
95 cm	8.3	6.4	8.3	8.3	7.9
C_{org} [%]					
5 cm	12.2	3.2	7.3	15.5	10.0
35 cm	1.8	0.8	3.6	9.2	8.1
65 cm	2.2	0.8	2.4	9.6	4.0
95 cm	2.3	0.5	1.7	8.8	3.7

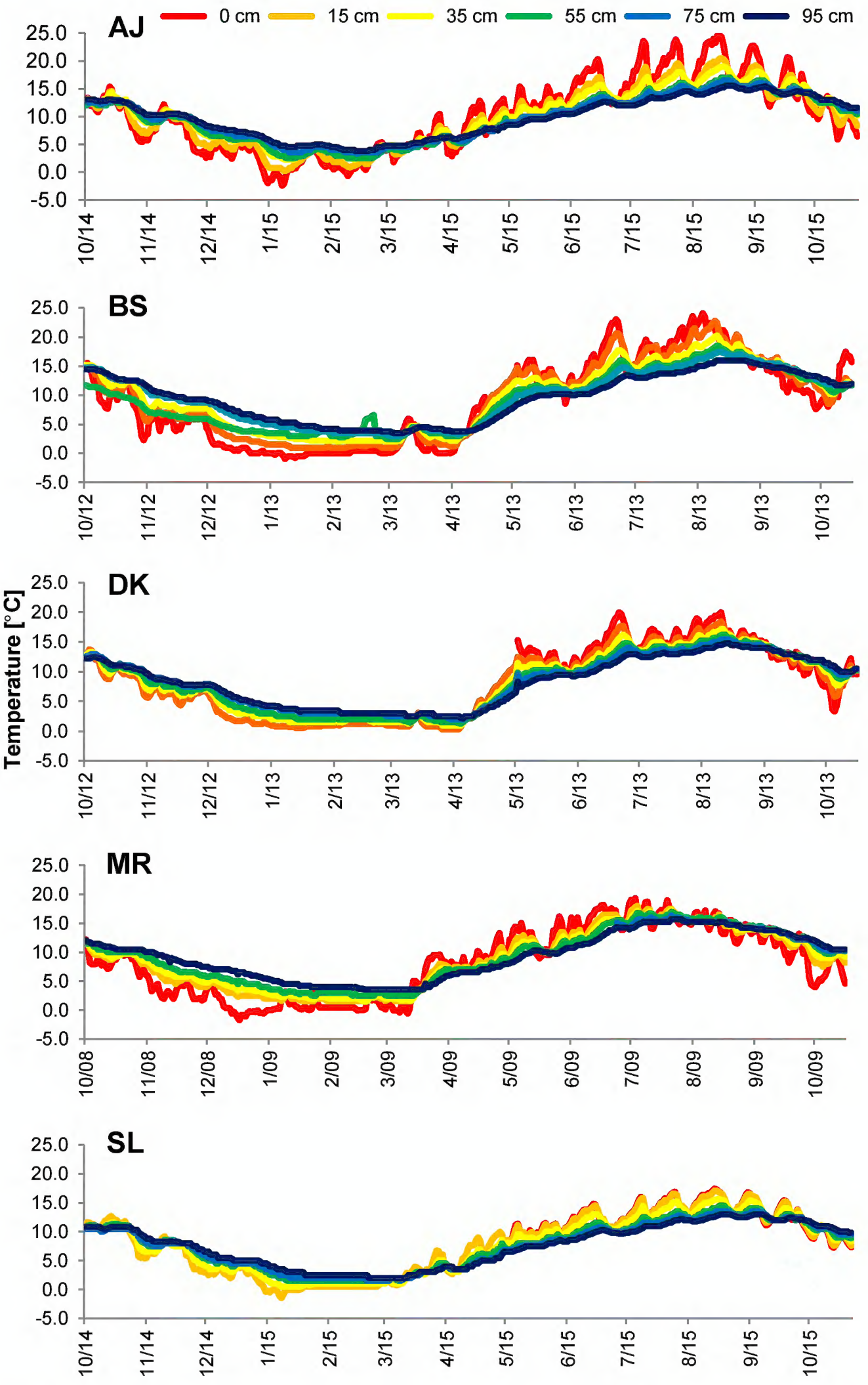

Figure 3. Monthly temperature fluctuations along the depth gradient of the investigated screes. Abbreviations: AJ – Ardovská jaskyňa Cave, BS – Belinské skaly Rocks, DK – Driencanský kras Karst, MR – Malý Ružínok Valley, SL – Silická ľadnica Cave.

Diversity and vertical distribution of Oribatida

In total, 909 individuals of oribatid mites belonging to 58 species were recorded at the study sites. The number of oribatids captured per trap ranged from 0 to 122, and the species richness from 0 to 37 (Appendix 1). We found very low oribatid numbers at all sites, except the Malý Ružínok Valley (MR), where 80% of all individuals were recorded. At the Ardovská jaskyňa Cave (AJ), the number of specimens captured was six-times less than at MR. The total number of individuals found at other localities was also very low, varying from 10 to 24 per study period (12 months). Total species richness was directly related to the number of individuals. The MR site showed the highest species richness, followed by AJ (Table 1, Appendix 1). Species richness at the other scree sites was very low.

The vertical distribution of oribatid mites reflected the distribution of organic carbon content in the soil along the vertical scree slope. The highest activity of oribatids was recorded in the upper soil layers and rapidly decreased with scree depth (Appendix1). The same pattern was registered in the number of species. At the Belinské skaly Rocks, Drienčanský kras Karst and Silická ľadnica Cave, almost all individuals were recorded at a depth of 5 cm, i.e. below the soil surface. The AJ site was characterized by a gradual decrease in activity from 15 to 55 cm and a slight increase at a depth of 85 cm. The species richness was constantly low from 15 cm downwards. At Belinské skaly Rocks (BS) and Silická ľadnica Cave (SL), Oribatida occurred only until the depth of 25 cm, and 45 cm respectively. In contrast, the Drienčanský kras Karst (DK) site revealed an activity gap from 25 to 45 cm depth. At MR, the highest proportions of individuals (90.1%) and species richness (90.2%) were recorded at 5 cm depth. The decrease in both species richness and activity was very marked between 5 and 15 cm, and from 25 cm downwards both community parameters had lower values, similarly as at the AJ site (Fig. 4; Appendix 1).

Three species – *Ceratoppia bipilis* (Hermann, 1804), *Scheloribates pallidulus* (C. L. Koch, 1841) and *Xenillus tegeocranus* (Hermann, 1804) – were trapped at three sites (AJ, DK and MR) and the genus *Phthiracarus* sp. was collected at four sites (AJ, DK, MR and SL). The most abundant species, *Chamobates voigtsi* (Oudemans, 1902), occurred only at the MR site. Based on the Starý's paper (2006), two new species were found for Slovakia: *Banksinoma lanceolata* (Michael, 1885) and *Oribatula amblyptera* Berlese, 1916. Both species were recorded only at the MR site, co-occurring with the eutroglophile *Pantelozetes cavatica* (Kunst, 1962).

Sites BS, DK and SL showed only few records of oribatid individuals. At the AJ site, the oribatid community was the most stratified across the depth gradient (Table 2). At this habitat, the highest degree of Bray-Curtis (quantitative) similarity was recorded between the depths of 15–25 cm (0.74) and 35–45 cm (0.75), respectively. The lowest quantitative similarity was observed between the depths of 5 cm and 75 or 95 cm (0.00 for both pairs). Additionally, the Sørensen (qualitative) similarity index confirmed that the depth of 5 cm was relatively dissimilar in species composition from the rest of the vertical profile. In contrast, the MR site showed no remarkable similarity pattern of the community among the particular depth layers.

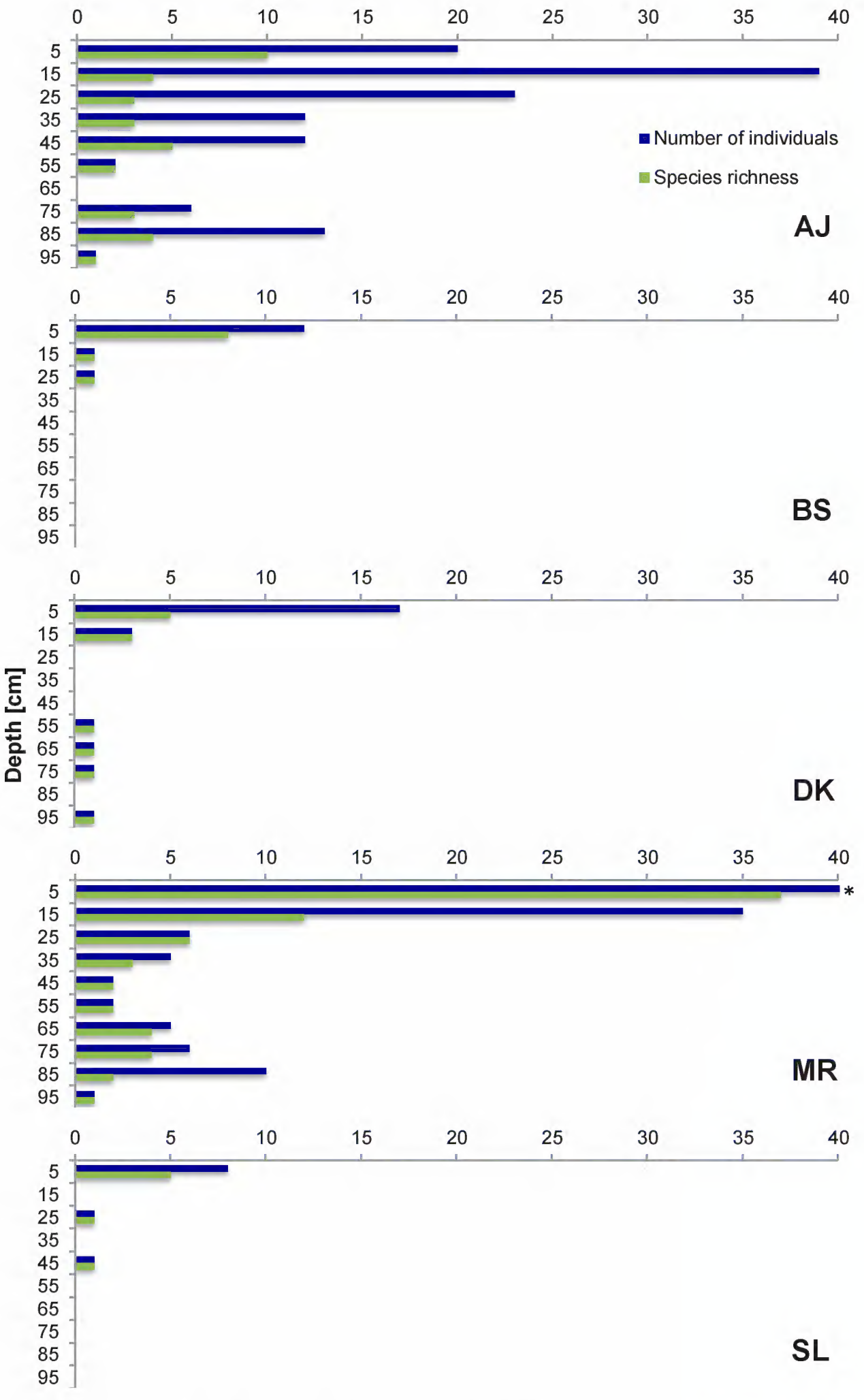

Figure 4. Distribution of Oribatida along the vertical profile of the screes expressed as a total number of trapped individuals and species richness. Abbreviations: AJ – Ardovská jaskyňa Cave, BS – Belinské skaly Rocks, DK – Drienčanský kras Karst, MR – Malý Ružínok Valley, SL – Silická ľadnica Cave, *Number of individuals = 661.

Table 2. Similarity of oribatid communities along the depth gradient at five scree slope sites. Above the diagonal: the Bray-Curtis index, below the diagonal: the Sørensen incidence-based index. Index values > 0.50 are indicated in bold. Value 1.00 indicates identical communities.

Ardovská jaskyňa Cave										
Depth	**5 cm**	**15 cm**	**25 cm**	**35 cm**	**45 cm**	**55 cm**	**65 cm**	**75 cm**	**85 cm**	**95 cm**
5 cm		0.34	0.37	**0.56**	0.44	0.18	0.00	0.15	0.48	0.10
15 cm	0.43		**0.74**	0.47	0.35	0.05	0.00	0.13	0.38	0.05
25 cm	0.31	**0.86**		**0.51**	0.40	0.08	0.00	0.07	**0.56**	0.08
35 cm	0.31	**0.86**	**1.00**		**0.75**	0.14	0.00	0.33	**0.64**	0.15
45 cm	0.27	**0.67**	**0.75**	**0.75**		0.14	0.00	0.44	0.48	0.15
55 cm	0.33	0.33	0.40	**0.40**	0.29		0.00	0.00	0.13	**0.67**
65 cm	–	–	–	–	–	–		0.00	0.00	0.00
75 cm	0.15	0.29	0.33	0.33	**0.50**	0.00	–		0.00	0.00
85 cm	0.29	**0.50**	**0.57**	**0.57**	0.44	0.33	–	0.29		0.14
95 cm	0.18	0.40	**0.50**	**0.50**	0.33	**0.67**	–	0.00	0.40	
Belinské skaly Rocks										
Depth	**5 cm**	**15 cm**	**25 cm**	**35 cm**	**45 cm**	**55 cm**	**65 cm**	**75 cm**	**85 cm**	**95 cm**
5 cm		0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
15 cm	0.22		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
25 cm	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00
35 cm	–	–	–		–	–	–	–	–	–
45 cm	–	–	–	–		–	–	–	–	–
55 cm	–	–	–	–	–		–	–	–	–
65 cm	–	–	–	–	–	–		–	–	–
75 cm	–	–	–	–	–	–	–		–	–
85 cm	–	–	–	–	–	–	–	–		–
95 cm	–	–	–	–	–	–	–	–	–	
Driencanský kras Karst										
Depth	**5 cm**	**15 cm**	**25 cm**	**35 cm**	**45 cm**	**55 cm**	**65 cm**	**75 cm**	**85 cm**	**95 cm**
5 cm		0.10	0.00	0.00	0.00	0.11	0.11	0.11	0.00	0.00
15 cm	0.25		0.00	0.00	0.00	**0.50**	**0.50**	**0.50**	0.00	0.00
25 cm	–	–		–	–	0.00	0.00	0.00	–	0.00
35 cm	–	–	–		–	0.00	0.00	0.00	–	0.00
45 cm	–	–	–	–		0.00	0.00	0.00	–	0.00
55 cm	0.29	**0.50**	–	–	–		0.00	0.00	0.00	0.00
65 cm	0.33	0.00	–	–	–	0.00		0.00	0.00	0.00
75 cm	0.33	0.00	–	–	–	0.00	0.00		0.00	0.00
85 cm	–	–	–	–	–	–	–	–		0.00
95 cm	0.00	0.00	–	–	–	0.00	0.00	0.00	–	
Malý Ružínok Valley										
Depth	**5 cm**	**15 cm**	**25 cm**	**35 cm**	**45 cm**	**55 cm**	**65 cm**	**75 cm**	**85 cm**	**95 cm**
5 cm		0.10	0.01	0.01	0.00	0.01	0.01	0.02	0.03	0.00
15 cm	0.49		0.10	0.10	0.05	0.11	0.00	0.25	0.18	0.00
25 cm	0.19	0.22		0.20	0.00	0.29	0.20	0.20	0.13	0.33
35 cm	0.10	0.27	0.22		**0.57**	0.00	0.00	0.20	0.13	0.33
45 cm	0.05	0.14	0.00	**0.80**		0.00	0.00	0.29	0.17	**0.67**
55 cm	0.10	0.29	0.25	0.00	0.00		0.00	0.29	0.00	0.00
65 cm	0.15	0.00	0.40	0.00	0.00	0.00		0.00	0.00	0.00
75 cm	0.20	**0.50**	0.20	0.29	0.33	0.33	0.00		0.00	0.00
85 cm	0.05	0.14	0.00	0.40	**0.50**	0.00	0.00	0.33		0.00
95 cm	0.00	0.00	0.00	**0.50**	**0.67**	0.00	0.00	0.00	0.00	

Silická ľadnica Cave										
Depth	**5 cm**	**15 cm**	**25 cm**	**35 cm**	**45 cm**	**55 cm**	**65 cm**	**75 cm**	**85 cm**	**95 cm**
5 cm		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
15 cm	–		0.00	–	0.00	–	–	–	–	–
25 cm	0.00	–		0.00	0.00	0.00	0.00	0.00	0.00	0.00
35 cm	–	–	–		0.00	–	–	–	–	–
45 cm	0.00	–	0.00	–		0.00	0.00	0.00	0.00	0.00
55 cm	–	–	–	–	–		–	–	–	–
65 cm	–	–	–	–	–	–		–	–	–
75 cm	–	–	–	–	–	–	–		–	–
85 cm	–	–	–	–	–	–	–	–		–
95 cm	–	–	–	–	–	–	–	–	–	

Discussion

Worldwide, there are only a few studies on Acari occupying shallow subterranean environments (Borges 1993, Arillo et al. 1994; Růžička and Zacharda 1994; Schlick-Steiner and Steiner 2000; Zacharda et al. 2005). Within Europe, previously published studies on Oribatida in MSS have been carried out in France, Romania and Spain (Cassagne et al. 2008; Sendra et al. 2014; Jiménez-Valverde et al. 2015; Nae and Ivan 2015; Nae and Băncilă 2017). However, they used a different type of pitfall traps, which were monitored for shorter period than one year. In Slovakia, several studies on Arthropoda from MSS habitats have been published (Rendoš et al. 2012, 2014, 2016a, 2016b; Mock et al. 2015; Rudy et al. 2018; Jureková et al. 2019), but the present study is the first one on Oribatida. Here we provide data on oribatid communities inhabiting 1m-deep profile of screes in 10 cm stratification gained during a one-year period at five sites differing in microclimate, soil parameters and bedrock.

Shallow subterranean habitats are highly dynamic in terms of environmental factors (Culver and Pipan 2010). In the present study, differences in environmental characteristics along a depth gradient have been observed mainly in temperature and organic carbon content, but also in soil pH. It is known that temperature can regulate oribatid communities directly or through its effect on moisture conditions, and moreover, it may become a factor essential for the existence of certain species (Jiménez-Valverde et al. 2015). A mean temperature along the depth profile of screes tends to decline and only small temperature fluctuations through the year are noticed in the deeper levels of these habitats (e.g., Pipan et al 2011; Rendoš et al. 2012, 2016b; Mammola et al. 2016; Jureková et al. 2019). This is in conflict with our findings, since an increase of mean temperature towards deeper horizons appeared at the three study sites (BS, DK, MR), although the general trend of temperature fluctuation during the year was the same at all sites. Rendoš et al. (2016b) noted a decrease of mean temperature along the depth profile for these three sites only during a half-year period (May – October), unlike to our one year study period (October – October). Therefore, the length of study period notably influence the interpretation

of temperature regime across the depth profile. Besides that, the two study slopes with a very similar temperature regime, i.e. BS and MR, with the range of temperature along a depth profile from 8.1 °C to 9.7 °C, visibly contrasted in Oribatida activity. Thus, internal scree temperature was not the factor that could substantially affect the oribatid numbers. Since the two most abundant sites had a very similar temperature regime, we may state that temperature was an important though not a main factor limiting the number of oribatid individuals. Another environmental factor that probably influences oribatid mite communities indirectly is soil pH, partly associated with the type of bedrock. The AJ and MR sites, with a high organic carbon content and slightly alkaline topsoil, clearly showed higher oribatid activities and vertical stratification of communities along the scree profile compared to the other sites. The litter quality affects the densities of soil macro-decomposers (Scheu et al. 2003; Salamon et al. 2005; Eisenhauer 2010) and activity and the biomass of soil microorganisms (Bååth and Anderson 2003; Dequiedt et al. 2011), which serve as a main food source for Oribatida (Behan-Pelletier 1999). Rapid limitation of food sources and open spaces along the vertical gradient presumably led to a more or less sudden decline of Oribatida activity and species diversity at individual screes. The total number of individuals and species richness of oribatids trapped inside the forested screes distinctly reflected the amount of organic residue along the vertical profile of the given site. Consequently, the microclimate, organic carbon content and soil pH in the topsoil layer seem to be crucial factors that determined oribatid diversity and distribution within a depth profile of the studied screes.

All sites with limestone bedrock were situated near caves, and we expected to find cave dwelling species in the subterranean traps. The eutroglophilous *Pantelozetes cavatica*, often found in Slovak caves in association with bat guano (Ľuptáčik and Miko 2003), was recorded only at the MR site. Since we found this species to inhabit deeper layers (35, 45 and 95 cm), it is probable that this species is also able to migrate between MSS habitats and caves under suitable environmental conditions. Furthermore, the eurytopic species *Dissorhina ornata* (Oudemans, 1900), known to inhabit karst caves in Slovakia (Ľuptáčik and Miko 2003), was registered only at the basalt Belinské skaly Rocks site in the upper soil layer.

The dominant species differed between the particular sites, but the occurrence of the majority of them was limited to the surface soil layer (5–15 cm). Several species (*Ceratoppia bipilis*, *Oppiella subpectinata* (Oudemans, 1900), *Oribatella calcarata* (C. L. Koch, 1835), *Xenillus tegeocranus*) showed the potential to colonize deeper scree horizons from the surface. *Chamobates voigtsi*, defined as a psychrophilous species preferring acid forest soils, although it is able to tolerate a wider range of factors (Miko 1986; Starý 2003), was the most abundant species at the study sites.

Compared to data on Collembola (Rendoš et al. 2016b; Jureková et al. 2019) from the same study sites, oribatid mites showed considerably lower activity. The use of subterranean pitfall traps seems to be an adequate method for comprehensive studies on Collembola or other more mobile soil invertebrates (Rendoš et al. 2016b; Jureková et al. 2019). However, it is not an effective sampling technique for Oribatida in the

MSS environment, since it estimates the abundance of the given arthropod taxon as a function of its activity during the sampling period and population density in the habitat (Brown and Matthews 2016).

Conclusions

The present study was the first attempt to cover the diversity and distribution of soil oribatid mites along a depth profile of forested scree slopes in the Western Carpathians. Communities of Oribatida with relatively poor abundance and species richness were found to dwell at the studied MSS sites. The exception was the Malý Ružínok Valley site with suitable microclimate conditions, where more abundant oribatid communities had a clear vertical stratification. Edaphic species were limited especially to the topsoil layers rich in organic carbon. The unique status of the MSS habitat is supported by the recording of the rare specialized eutroglophilous species, *Pantelozetes cavatica*. The presence of this species relatively close to the scree surface underlines a function of MSS habitats as corridors for migration of subterranean oribatids towards the soil and surface dwellers to deeper subterranean spaces. Among the soil parameters measured, organic carbon content in the soil and soil pH were the governing factors affecting the diversity and vertical distribution of oribatid mites in the forested screes.

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Appendix 1

List of Oribatida species collected in the vertical gradient of the study screes.

Table 3.

Species	Ardovská jaskyňa Cave											Belinské skaly Rocks											Driencanský kras Karst											Malý Ružínok Valley											Silická ľadnica Cave										
Vertical gradient [cm]	5	15	25	35	45	55	65	75	85	95	Σ	5	15	25	35	45	55	65	75	85	95	Σ	5	15	25	35	45	55	65	75	85	95	Σ	5	15	25	35	45	55	65	75	85	95	Σ	5	15	25	35	45	55	65	75	85	95	Σ
Achipteria coleoptrata (Linné, 1758)	3	1	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
Achipteria nitens (Nicolet, 1855)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	2
Adoristes ovatus (C. L. Koch, 1839)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Banksinoma lanceolata (Michael, 1885)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Camisia spinifer (C. L. Koch, 1835)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–	1	–	–	–	2	–	–	–	5	–	–	–	–	–	–	–	–	–	–
Carabodes femoralis (Nicolet, 1855)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
Carabodes labyrinthicus (Michael, 1879)	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Carabodes ornatus Storkan, 1925	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–
Carabodes rugosior Berlese, 1916	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Carabodes tenuis Forsslund, 1953	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	1	–	–	–	–	–	–	–	–	11	–	–	–	–	–	–	–	–	–	–
Ceratoppia bipilis (Hermann, 1804)	2	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	1	–	–	5	6	–	–	–	–	–	1	–	–	–	7	–	–	–	–	–	–	–	–	–	–
Ceratoppia quadridentata (Haller, 1882)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	1	–	–	–	–	–	–	–	–	8	–	–	–	–	–	–	–	–	–	–
Ceratozetes peritus Grandjean, 1951	–	–	–	–	–	–	2	2	–	4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Chamobates pusillus (Berlese, 1895)	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	3	–	–	–	–	–	1	–	–	–	4	–	–	–	–	–	–	–	–	–	–
Chamobates spinosus Sellnick, 1928	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–
Chamobates voigtsi (Oudemans, 1902)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	335	12	1	1	–	–	–	–	–	–	349	–	–	–	–	–	–	–	–	–	–
Damaeus gracilipes (Kulczynski, 1902)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–
Damaeus riparius Nicolet, 1855	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9	–	–	–	–	–	–	–	–	–	9	–	–	–	–	–	–	–	–	–	–
Dissorhina ornata (Oudemans, 1900)	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Species	Ardovská jaskyňa Cave												Belinské skaly Rocks												Driečanský kras Karst												Malý Ružínok Valley												Silická ľadnica Cave											
Vertical gradient [cm]	5	15	25	35	45	55	65	75	85	95	Σ		5	15	25	35	45	55	65	75	85	95	Σ		5	15	25	35	45	55	65	75	85	95	Σ		5	15	25	35	45	55	65	75	85	95	Σ		5	15	25	35	45	55	65	75	85	95	Σ
Eueremaeus oblongus (C. L. Koch, 1835)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–
Eueremaeus silvestris (Forsslund, 1956)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–
Eupelops hirtus (Berlese, 1916)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		3	1	–	–	–	–	–	–	–	–	4		–	–	–	–	–	–	–	–	–	–	–
Eupelops plicatus (C. L. Koch, 1835)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		7	–	1	–	–	–	–	–	–	–	8		–	–	–	–	–	–	–	–	–	–	–
Euphthiracarus cribrarius (Berlese, 1904)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		2	–	–	–	–	–	–	–	–	–	2		–	–	–	–	–	–	–	–	–	–	–
Euzetes globulus (Nicolet, 1855)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–
Fosseremus laciniatus (Berlese, 1905)	1	–	–	–	–	1	–	–	–	–	2		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Galumna lanceata (Oudemans, 1900)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		6	–	–	–	–	–	–	–	–	–	6		–	–	–	–	–	–	–	–	–	–	–
Gustavia microcephala (Nicolet, 1855)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Heminothrus targionii (Berlese, 1885)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		2	–	–	–	–	–	–	–	–	–	2		–	–	–	–	–	–	–	–	–	–	–
Hermanniella dolosa Grandjean, 1931	–	–	–	–	2	–	–	–	–	–	2		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Liacarus subterraneus (C. L. Koch, 1841)	–	3	2	1	1	–	–	–	1	–	8		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1
Metabelba pulverosa Strenzke, 1953	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		6	–	–	–	–	–	–	–	–	–	6		–	–	–	–	–	–	–	–	–	–	–
Multioppia laniseta Moritz, 1966	–	–	–	–	–	–	–	–	–	–	–		–	1	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Oppia denticulata (R. & G. Canestrini, 1882)	–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Oppiella (Oppiella) nova (Oudemans, 1902)	–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Oppiella (Rhinoppia) obsoleta (Paoli, 1908)	–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Oppiella (R.) subpectinata (Oudemans, 1900)	7	28	20	7	5	1	–	–	9	1	78		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Oribatella calcarata (C. L. Koch, 1835)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		21	4	–	1	1	–	–	3	9	–	39		1	–	–	–	–	–	–	–	–	–	1
Oribatula amblyptera Berlese, 1916	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		8	–	–	–	–	–	–	–	–	–	8		–	–	–	–	–	–	–	–	–	–	–
Oribatula tibialis (Nicolet, 1855)	–	–	–	–	–	–	–	–	–	–	–		3	–	–	–	–	–	–	–	–	–	3		–	–	–	–	–	–	–	–	–	–	–		45	1	–	–	–	–	–	1	–	–	47		–	–	–	–	–	–	–	–	–	–	–

Species	Ardovská jaskyňa Cave												Belinské skaly Rocks												Drienčanský kras Karst												Malý Ružínok Valley												Silická ľadnica Cave											
Vertical gradient [cm]	5	15	25	35	45	55	65	75	85	95	Σ		5	15	25	35	45	55	65	75	85	95	Σ		5	15	25	35	45	55	65	75	85	95	Σ		5	15	25	35	45	55	65	75	85	95	Σ		5	15	25	35	45	55	65	75	85	95	Σ
Pantelozetes cavatica (Kunst, 1962)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	3	1	–	–	–	–	1	5		–	–	–	–	–	–	–	–	–	–	–
Phthiracarus spp.	–	–	–	–	1	–	–	1	–	–	2		–	–	–	–	–	–	–	–	–	–	–		4	–	–	–	–	–	1	–	–	–	5		11	–	–	–	–	–	–	–	–	–	11		1	–	–	–	–	–	–	–	–	–	1
Pilogalumna tenuiclava (Berlese, 1908)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		20	3	–	–	–	1	–	–	–	–	24		–	–	1	–	–	–	–	–	–	–	1
Platynothrus peltifer (C. L. Koch, 1839)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		22	1	1	–	–	1	–	1	–	–	26		2	–	–	–	–	–	–	–	–	–	2
Poroliodes farinosus (C. L. Koch, 1840)	1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Punctoribates punctum (C. L. Koch, 1839)	–	–	–	–	–	–	–	–	–	–	–		2	1	–	–	–	–	–	–	–	–	3		7	–	–	–	–	–	–	–	–	–	7		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Scheloribates (Hemileius) initialis (Berlese, 1908)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		3	–	–	–	–	–	–	–	–	–	3		–	–	–	–	–	–	–	–	–	–	–
Scheloribates laevigatus (C. L. Koch, 1835)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		6	–	–	–	–	–	–	–	–	–	6		–	–	–	–	–	–	–	–	–	–	–
Scheloribates latipes (C. L. Koch, 1844)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Scheloribates pallidulus (C. L. Koch, 1841)	1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	1		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–
Scheloribates quintus Wunderle, Beck & Woas, 1990	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		42	4	–	–	–	–	–	–	–	–	46		–	–	–	–	–	–	–	–	–	–	–
Spatiodamaeus fageti (Bulanova-Zachvatkina, 1957)	1	–	–	–	–	–	–	–	–	–	1		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–
Steganacarus (Tropacarus) carinatus (C. L. Koch, 1841)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		2	–	–	–	–	–	–	–	–	–	2
Tectocepheus velatus sarekensis Trägardh, 1910	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	1	–	–	–	1	–	–	–	2		–	–	–	–	–	–	–	–	–	–	–
Tritegeus bisulcatus Grandjean, 1953	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–
Xenillus tegeocranus (Hermann, 1804)	2	7	1	4	3	–	–	3	–	–	20		–	–	–	–	–	–	–	–	–	–	–		1	1	–	–	–	1	–	–	–	–	3		8	4	–	–	–	–	–	1	–	–	13		–	–	–	–	–	–	–	–	–	–	–
Zetorchestes falzonii Coggi, 1898	1	–	–	–	–	–	–	–	1	–	2		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		61	2	–	–	–	–	–	–	–	–	63		–	–	–	–	–	–	–	–	–	–	–
Zygoribatula exilis (Nicolet, 1855)	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–	–	–	–	–	–		1	–	–	–	–	–	–	–	–	–	1		–	–	–	–	–	–	–	–	–	–	–
Number of individuals	20	39	23	12	12	2	0	6	13	1	128		12	1	1	0	0	0	0	0	0	0	14		17	3	0	0	0	1	1	1	0	1	24		661	35	6	5	2	2	5	6	10	1	733		8	0	1	0	1	0	0	0	0	0	10
Species richness	10	4	3	3	5	2	0	3	4	1	14		8	1	1	0	0	0	0	0	0	0	9		5	3	0	0	0	1	1	1	0	1	8		37	12	6	3	2	2	4	4	2	1	41		5	0	1	0	1	0	0	0	0	0	7